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Seed production studies are needed to round out our knowledge of factors affecting natural regeneration in Engelmann spruce. An adequate supply of viable seed is one of the three elements essential to successful seedling establishment; namely, ample seed supply, receptive seedbed, and favorable growing conditions. Good seedbed and favorable climatic conditions are ineffective if the required amount of viable seed is not provided.

A survey of the factors affecting seedling establishment in the Engelmann spruce-subalpine fir type in the Intermountain Region[1] shows that seedlings have been limited to the margins of openings in close proximity to seed sources--usually within 3 to 6 chains. Is the limited distribution of seedlings in relation to seed source caused by a lack of seed production? This basic question can only be answered by detailed studies of seed production and dissemination. This report describes the establishment and early results of several seed production studies. Seed quantity, quality, and dispersal are being measured annually, but only results from the 1964 seed year are reported here.

PAST WORK

Few studies of Engelmann spruce seed production in the Northern and Intermountain Regions are recorded. In the first of these studies, Boe[2] analyzed rangers' seed reports in Montana for the period 1908 to 1953. He reported data separately for the area east and west of the Continental Divide. Crops were rated as good, fair, and poor, based upon visual estimates made by National Forest Rangers each year. West of the Divide, five good, eight fair, and nine poor crops were shown for a 22-year reporting period. East of the Divide, seed production was considerably lower, and only two good, four fair, and 15 poor crops were reported during a 21-year period. Throughout the State, 1926 and 1952 were both exceptionally good spruce years. In 1952, the spruce seed crop was bountiful throughout the Northern Rockies and Intermountain areas.

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[1]Roe, Arthur L., and Wyman C. Schmidt. Factors affecting natural regeneration of spruce in the Intermountain Region. U.S. Forest Serv., Intermountain Forest and Range Exp. Sta., mimeo. report, 68 pp., illus. (In cooperation with the Ashley, Dixie, Payette, Teton, and Uinta National Forests.) 1964.

[2]Boe, Kenneth N. Periodicity of cone crops for five Montana conifers. Mont. Acad. Sci. Proc. 14: 5-9. 1954.

Squillace[3] has shown that in 1952 significant spruce seed dispersal (60,000 sound seed per acre) reached out as far as 9 chains from the timber edge in a large spruce clearcut block in western Montana. However, he points out that this seed dispersal occurred during a bumper seed year. During a poorer seed crop year, the quantity to reach the center of the 18- by 30-chain clearcutting would have been proportionately lower.

Germinative capacity of spruce seed has been studied by Curtis,[4] who collected samples from the Boise, Bridger, Dixie, Fishlake, Manti-LaSal, Payette, Targhee, and Uinta Forests. Values for partially cleaned seed ranged from 50 to 70 percent. Curtis reported that some of the 1955 seed from the Fishlake and Dixie National Forests had been infested with unidentified insects, so that the viability values were slightly lowered.

STUDY METHOD

Two methods were employed to investigate seed production in this study: (1) seed traps to measure quantity of seed and distance the seed is dispersed, and (2) external morphological studies to determine past cone production in relation to the current year's production. The methods will be discussed separately below.

SEED TRAP STUDIES[5]

Seed traps were located in three areas, namely: (1) the Aquarius Plateau or "Griffin Top" on the Dixie National Forest, (2) the Togwotee Pass area on the Teton National Forest, and (3) the Fisher Creek burn on the Payette National Forest. At each location twenty 2- by 3-foot seed traps were placed in two rows about 2 chains apart and oriented at right angles to the timber edge. The first trap in each row was placed 1 chain into the timber from the edge of the opening; the second trap was placed at timber edge. Traps 3 to 8 were placed at 1-chain intervals and traps 9 and 10 were placed at 2-chain intervals. The last trap (number 10) was placed 10 chains from the timber edge except on the Togwotee Pass area. There, because the only suitable opening was narrow, all traps were placed at 1-chain intervals and the last trap was located 8 chains out from the timber edge. This trap placement enabled us to measure

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[3]Squillace, A. E. Engelmann spruce seed dispersal into a clearcut area. U.S. Forest Serv., Intermountain Forest and Range Exp. Sta. Res. Note 11, 4 pp., illus. 1954.

[4]Curtis, James D. Germinative capacity of Engelmann spruce seed. U.S. Forest Serv., Intermountain Forest and Range Exp. Sta. Res. Note 58, 3 pp. 1958.

[5]The author is grateful to National Forest Administration personnel in the Timber Management Division of the Regional Office and the various National Forests of Region 4 for their interest in this study and the valuable cooperation they gave in locating study areas, constructing seed traps, and making seed collections. Their assistance allowed earlier scheduling of the study than might otherwise have been possible.

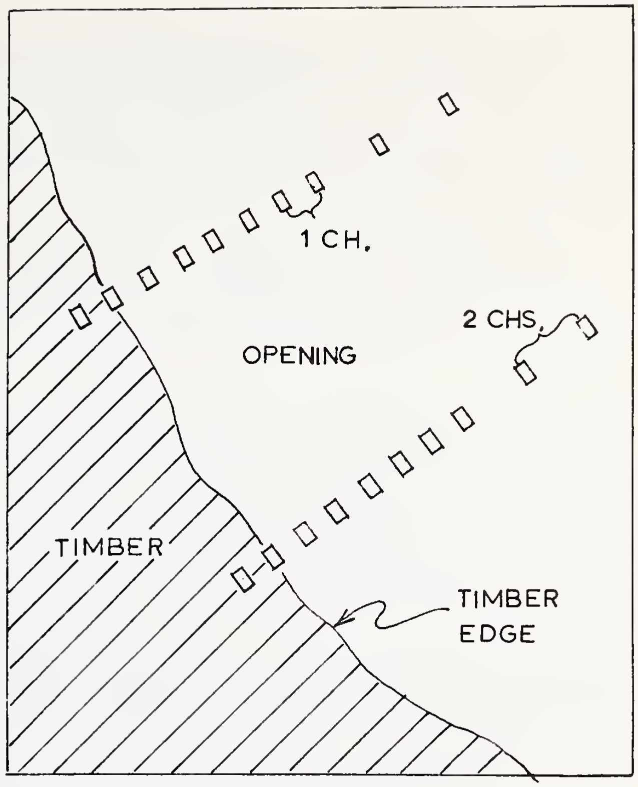

Figure 1.--Seed trap layout.

seed dissemination within the timber, at timber edge, and at intervals out to 8-10 chains from the timber edge. A typical seed trap layout is illustrated in figure 1.

Seed trap contents were collected at approximately 2-week intervals beginning on September 15 until snowfall interfered. The last collection was made in July 1965 to include overwinter seedfall.

The quality of the seed collected in the seed traps was determined by cutting tests that showed which seeds were hollow or contained shriveled or dead embryos and which were filled and appeared sound. Estimates of total quantities of seed produced were based on the sound seed yield.

EXTERNAL MORPHOLOGICAL STUDIES[6]

Engelmann spruce cones are usually initiated in the terminal position on branches and twigs and mature in 1 year. At the end of the season the cones may be shed, leaving a cone scar consisting of a rosette of basal cone scales adhering to the branch; alternatively, the cone may persist for several years after it opens and the seed is shed. The age of the cone scars may be determined by a study of the branchlet development. Cones are always borne on the terminal end of the previous year's wood; for

[6]For a more detailed discussion of the morphological method see Gorchakovskii, P. L. Novel methods of investigating the dynamics of seed production in conifers. Botanasheskii Zhurnal 43: 1445-1459, illus. 1958.

example, 1964 cones were developed in a terminal position on 1963 wood. The buds formed during the 1964 growing season and fully differentiated into staminate, ovulate, and vegetative buds by the end of that growing season provided the flowers and foliage for 1965. Therefore the 1965 cones, which were present within 1964 terminal buds, developed on the end of 1964 wood.

Cone scars can be reliably identified and dated as long as 3 years after the cones have been shed. Consequently, examination of sample branches from spruce crowns provides a basis for determining past cone production relative to the current year's production.

Trees were sampled on four cutting areas: (1) Coyote Hollow Sale, Dixie National Forest; (2) Togwotee Pass, Teton National Forest; (3) Pearl Creek Sale, Teton National Forest; and (4) Wolf Creek Summit road clearing, Uinta National Forest. Felled trees in the cuttings were picked randomly except that some were not usable because their crowns broke up so badly when they struck the ground that the desired branch samples were not available. Sample branches were collected by first dividing the upper 10 feet of the crown length into five 2-foot sections and then choosing one sample branch at random, if possible, from each 2-foot length. The branches were placed in plastic bags and taken to the laboratory for counting of cone scars. Samples were collected from 5 to 10 trees in each stand.

The method of sampling had been determined earlier as follows: statistics for each sample were compiled for the upper 10 feet (five sample branches) and compared with the samples from a 20-foot section (10 sample branches in each tree) on the first two areas sampled. The distribution or cone production frequency by years (1961 to 1964) did not differ significantly in the five-branch-per-tree sample from that in the 10-branch sample, as shown by chi-square tests. The upper 10 feet of the tree crowns produced about 89 percent of the cones and cone scars sampled. Thus, five branches taken from the upper 10 feet of the crown provide as good an estimate of relative distribution over the years as a sample of 10 branches taken from the upper 20 feet. Therefore, all sampling in the study was based upon five branches selected in the upper 10 feet of the crown.

RESULTS

1964 SEED YEAR

High production.--Engelmann spruce seed trees bore an abundant seed crop in 1964. Highest production measured in this study occurred on the Teton Forest in the Togwotee Pass area. Table 1 shows seed production as measured in the timber by location. For comparison, seed production in the Falls Creek area on the Flathead National Forest for the bumper seed year 1952 is included. The 1964 crop year, on the Teton Forest at least, was as productive as the 1952 year on the Flathead Forest.

Table 1.--Engelmann spruce seed dispersed in the timber within 1 chain of the cutting edge

Forest and area	Year	Basal area of seed trees per acre d.b.h. 10 in. and larger	Estimated sound seed per acre	Confidence limit P = .95
		Square feet		
Teton:				
Togwotee Pass	1964	[1]193	2,015,376	±1,119,937
Dixie:				
Griffin Top	1964	67	592,416	±465,801
Payette:				
Fisher Creek burn	1964	36	199,408	±198,091
Flathead:				
Falls Creek	1952	(2)	842,000	±349,600

[1]Basal area was determined by Bitterlich method. Standard errors were considered too small to be of concern.

[2]The basal area of the seed source was not measured in 1952, but in the author's recollection of the stand it would have been comparable to that on the Teton area.

The quantity of seed produced is proportional to the square feet of basal area per acre in spruce trees 10 inches and larger in diameter at breast height (basal area is used to integrate number and size). The basal areas of seed trees on the Dixie (Griffin Top) and Payette (Fisher Creek burn), 36 and 67 square feet, respectively, fall considerably below the 193 square feet measured on the Teton (Togwotee Pass area) as shown in table 1. Seed production on the Togwotee Pass area was nearly 5 times as heavy as on the Griffin Top area and almost 12 times as heavy as on the Fisher Creek burn.

Seed quality.--Differences in seed quality also contributed to the variability of sound seed production. Of the three locations studied, the Togwotee Pass area on the Teton showed not only the highest seed production, but also the highest proportion of sound seed. Soundness of the 1952 seed on Falls Creek of the Flathead Forest corresponded closely with that of the Teton Forest in 1964. The percent of filled seed is tabulated below:

Area	Filled seed as a percent of total seed
Togwotee Pass	57.4 ± 0.84
Griffin Top	29.6 ± 2.27
Fisher Creek burn	55.6 ± 2.76
Falls Creek (1952)	58.9 ± .89

As the tabulation shows, the seed dispersed on the Griffin Top area on the Dixie National Forest showed the lowest percent of filled seed; the quality of the seed in the Fisher Creek burn area of the Payette Forest fell only slightly below that of the Togwotee Pass area of the Teton Forest.

Efficiency of the seed source.--The average tree on the Togwotee Pass area produced nearly twice as many sound seeds per square foot of basal area as the average tree on the Fisher Creek burn. Nearly equal amounts of sound seed were produced by average trees on the Togwotee Pass and Griffin Top areas. Although the basal area contained in seed trees varied from 36 to 193 square feet per acre of Engelmann spruce (table 1), relative production of the average tree can be determined by dividing the number of sound seeds per trap by the seed tree basal area per acre. (The calculation was based on seeds caught in the timber and at timber edge.) This method provides an index value expressed as the number of seeds caught per square foot of basal area in seed trees 10 inches d.b.h. and larger. If the seed trees in all the areas produced seed with equal efficiency, a uniform rate or index should result. However, as can be seen from the following tabulation, the seed source on the Fisher Creek burn was least effective, whereas the seed sources on the Griffin Top and Togwotee Pass areas were nearly equally effective.

Area	Number of seeds caught per sq. ft. basal area	Confidence limit P = .95
Togwotee Pass	1.35	± 0.75
Griffin Top	1.14	± .90
Fisher Creek burn	.72	± .71

Seed dispersal.--Seed dispersal into clearings or openings from the timber edge follows an exponential distribution. Regression lines were fitted to the data collected from seed traps on the three areas studied in the autumn of 1964 and the spring of 1965 and also the data collected in Falls Creek on the Flathead Forest for the 1952 seed crop. The regression equations are summarized below.

Area	S.E. of y	r
1. Griffin Top (1964)		
$\log_e \hat{y} = 4.299 - 0.475\,(D+2)$	1.17470	0.818
2. Togwotee Pass (1964)		
$\log_e \hat{y} = 5.762 - 0.280\,(D+2)$	.21200	.970
3. Fisher Creek burn (1964)		
$\log_e \hat{y} = 3.364 - 0.313\,(D+2)$	.81200	.805
4. Falls Creek (1952)		
$\log_e \hat{y} = 5.845 - 0.294\,(D+2)$	.43740	.921

Where

$\log_e \hat{y}$ = Logarithm of number of seeds per trap

D+2 = Distance from timber edge in chains plus 2. The constant 2 was added to the distance to avoid 0 distance for the traps at timber edge and -1 chain for the traps 1 chain into timber.

The individual regressions for each location have been maintained independently although the regression coefficients (slopes) all appear to be similar. A covariance analysis summarized in table 2 shows that the coefficients are significantly different at the 5-percent level. On the other hand, the differences between adjusted means are significant at the 1-percent level. A large share of the difference associated with the adjusted means is the result of large differences in the size (basal area) of the seed source. The analysis could end here with individual curves for each area. However, the fact that the difference in coefficients was barely significant at the 5-percent level (an F value of 3.26 against a tabular value of 3.17) would indicate that the coefficients were not much more variable than could be expected from chance distribution. Therefore, the hypothesis that a common regression coefficient for spruce seed dispersal exists is not disproven. This is especially true since some of the variance may be due to factors not dealt with nor identified, such as the effect of slope and wind direction.

Table 2.--Summary of covariance analysis for three areas

Source of variation	D.f.	Deviations from regression		
		Sum of squares	Mean square	F.
Within groups	54	37.51481	0.69472	
Regression coefficient	2	4.53317	2.26658	3.262 significant
Common regression	56	42.04798	.75085	
Adjusted means	2	87.81965	43.90982	58.48014 highly significant
Total	58	129.86763		

A multiple regression was worked out in which (1) the distance from seed source and (2) the basal area of the seed source were employed as independent variables. The following multiple regression equation resulted:

$$\text{Log}_e \hat{y} = 4.66094 - .35353 (D+2) + .01772 \text{ B.A}$$

Where D+2 = Distance from timber edge in chains plus 2

B.A. = Basal area of spruce seed trees 10 inches d.b.h. and larger in square feet

$\text{Log}_e \hat{y}$ = Natural logarithm of seed per acre in thousands.

The following analysis is a breakdown of the variation associated with each of the variables.

Source of variation	D.f.	Sum of squares	Mean square	R^2	F.
D+2	1	80.11156	80.11156	0.3769	**108.587
B.A. (added effect)	1	90.39984	90.39984	.4252	**122.532
Regression	2	170.51140	85.25570	.8021	**115.56
Error	57	42.05260	.73776		
Total	59	212.56400			

** Indicates a highly significant relationship.

The analysis demonstrates the importance of the size of seed source as well as the distance from timber edge in determining the amount of seed dispersed. The equation is not recommended for prediction because the covariance analysis shows that the curves differ in slope as well as elevation according to the different areas sampled. Table 3 shows the estimated seed production based upon the independent regression equations for each area.

Table 3.--Estimated sound spruce seed per acre[1] according to distance from timber edge

Distance from timber edge (D)	Number of seeds per acre: Fisher Creek burn 1964	Togwotee Pass 1964	Griffin Top 1964	Falls Creek 1952
Chains				
-1	153,476	1,783,278	370,096	1,029,600
0	112,240	1,349,147	230,300	771,200
1	82,183	1,019,652	143,351	571,600
2	60,084	771,047	89,211	426,000
3	43,959	582,923	55,498	317,360
4	32,155	440,810	35,345	236,480
5	23,522	333,279	21,495	176,240
6	17,206	251,945	13,375	131,320
7	12,589	190,498	8,250	97,840
8	9,155	144,043	5,179	72,920
9	6,737	108,941	3,188	55,960
10	4,929	82,374	2,006	40,480

[1]The values shown were derived by using the regression equations on page 6 and upper 7 to get values per seed trap for each distance. These values were converted to per-acre figures by using the appropriate converting factor for each area.

Time of seed fall.--The period of greatest seed fall varied among the three study areas. Only minor amounts of sound seed--less than a maximum of 5 percent--fell on any of the areas prior to mid-September. From two-thirds to more than three-fourths of the total sound seed was released from trees on the Fisher Creek burn and Togwotee Pass areas, respectively, by October 20. Seed fall on the Griffin Top occurred much later; there only slightly more than one-third or 39 percent of total sound seed was dispersed by October 20. Table 4 shows the percent of total sound seed collected in each collection period.

FOUR YEAR CONE PRODUCTION

The cone crop produced in 1964 ranged from 2 to about 13 times greater than the annual crops for the last 3 years, as determined by cone scar counts. Table 5 shows the relative cone production on spruce trees from the four areas sampled. The minor differences between the four sample distributions were shown by test of independence to be significant. On the basis of these four samples of cone crops, we can rate 1964 as an excellent seed year and 1961 to 1963 as poor to moderate years. The two samples for 1965 suggest that it was a moderate seed year.

Table 4.--Proportion of total seed dispersed, by collection periods

(In percent)

Area	Period					Total
	Sept. 15-17 1964	Oct. 1-6 1964	Oct. 13-20 1964	Oct. 30 1964	July 1-22 1965	
Togwotee Pass	5.32	72.53	([1])	([1])	22.15	100.00
Fisher Creek burn	1.10	37.57	28.73	15.47	17.13	100.00
Griffin Top	.49	9.16	29.21	([1])	61.14	100.00

[1] Inclement weather, including snow, prevented collections.

Table 5.--Relative cone production by years expressed as percent of 1964 base year

Year	Teton N.F. Togwotee Pass	Dixie N.F. Coyote Hollow	Payette N.F. Pearl Creek	Uinta N.F. Wolf Creek Summit
1965	([1])	([1])	95.1	39.1
	[2] 100.0	100.0	100.0	100.0
1963	30.1	29.1	33.3	50.0
1962	26.5	13.1	15.2	21.4
1961	15.7	9.9	12.4	7.7

[1] Counts of cone scars were made prior to 1965 seed year on these locations.

[2] Groups of percentages, included within brackets are shown by Duncan Multiple Range Test to be significantly different from other groups for that location, at 5-percent level of probability, but the individual percentages are not different from others in the same group. For example, in Pearl Creek 1961-1963 cone crops were significantly different from 1964 and 1965 cone crops.

This study, however, tells us nothing about the quality of the seeds produced within these cones. We can only assume that seed production was somewhat proportional to cone production. Usually poorer quality seed is disseminated in the years of light seed production and higher quality seed in good seed years. The reliability of the estimates for the years prior to 1964 is not known. The possibility that squirrels removed cones, thus eliminating cone scars, and the effect of high winds, which shake out residual cone scars, cannot be measured.

DISCUSSION

The 1964 seed year can be classed as a bumper spruce seed year throughout most of the natural range of spruce in the Intermountain region. That year rates as the best out of 5 years, on the basis of evidence revealed in this study. The study shows that despite the large seed crop produced in 1964, some cones were also produced in each of the other years during the period 1961 to 1965.

Foresters design regeneration cuttings to ensure an adequate seed supply over the seedbed. This requires a knowledge of the quantity and quality of seed dispersed, annual variations in production, and the pattern of dispersal. These must be measured to provide statistics that will be useful in determining the most advantageous size and shape for clearcuttings. The study reveals that sound seed is dispersed in considerable quantities (0.5 to 4.6 percent of seed released in the timber) to a distance of 10 chains from the timber edge. The pattern of seed dispersal was found to be quite similar in all areas except for quantitative differences caused largely by differences in the seed sources, and possibly by minor topographic variations. However, it must be remembered that 1964 seed production was above average. Therefore, both quantities of seed produced and dispersal distances may be smaller in other years. One good seed year such as 1964 may account for as much seed production as the sum of 3 to 5 poorer years. Additional data will be required to work out the relationships of annual variations in seed production and patterns of dispersal.

What is an adequate quantity of seed? The answer to this question depends on the probability of seedling establishment. It is obvious that tons of seed dispersed over unreceptive seedbeds are wasted. However, where seedbeds are favorable, the desired quantity of seed may be determined from estimates of the numbers of sound seed required to establish each first-year seedling and the number of seedlings required to stock the seedbed. Germination and seedling survival studies on various types of seedbeds and in various topographic situations would provide probability estimates of seedling establishment and enable the forester to determine the effective seeding distances (the distance from timber edge to which acceptable minimum stocking can be expected under prevailing conditions). The size of openings should be determined by effective seeding distances rather than maximum seed dispersal distances.

Roe, Arthur L.
1967. Seed dispersal in a bumper spruce seed year. U.S. Forest Serv. Res. Paper INT-39, 10 pp., illus.

Spruce trees in the Intermountain region produced a bumper seed crop in 1964, as revealed by seed trap studies and cone scar counts. The extent of dispersal of this seed into openings in the timber stand was largely determined by the quantity and condition of the seed source bordering the openings, and by the distance of the seed source from the timber margin. Although large quantities of seed were released at the timber edge, an amount equal to less than 5 percent of this seed was dispersed as far as 10 chains into openings. The dispersal pattern away from the timber edge very closely followed an exponential distribution. The cone crop in 1964 ranged from 2 to 13 times greater than the comparable annual crops produced in the previous 3 years on the study areas.

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Headquarters for the Intermountain Forest and Range Experiment Station are in Ogden, Utah. Project headquarters are also at:

- Boise, Idaho
- Bozeman, Montana (in cooperation with Montana State University)
- Logan, Utah (in cooperation with Utah State University)
- Missoula, Montana (in cooperation with University of Montana)
- Moscow, Idaho (in cooperation with the University of Idaho)
- Provo, Utah (in cooperation with Brigham Young University)

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